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Update article

Visual perception is dependent on visuospatial working memory and thus on the posterior parietal cortex

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ABSTRACT

Visual perception involves complex and active processes. We will start by explaining why visual perception is dependent on visuospatial working memory, especially the spatiotemporal integration of the perceived elements through the ocular exploration of visual scenes. Then we will present neuropsychology, transcranial magnetic stimulation and neuroimaging data yielding information on the specific role of the posterior parietal cortex of the right hemisphere in visuospatial working memory. Within the posterior parietal cortex, neuropsychology data also suggest that there might be dissociated neural substrates for deployment of attention (superior parietal lobules) and spatiotemporal integration (right inferior parietal lobule).

1. Characteristics of the cortical representation of visual scenes

Today, neurosciences can yield crucial information on how space and body are represented in the brain. Visual information seen through the eyes is directed to the primary visual cortex at the level of the occipital cortex. At this level, data stemming from the right side of the visual field are sent to the left hemisphere, and vice versa. This first characteristic means that the visual scene is divided into two parts, each treated by different cortical hemispheres, grouping signals from both eyes according to their spatial origin. According to the presence of continuous eye movements to explore the visual scene, a given point in this scene can, with each eye movement, be sent alternatively to one brain hemisphere or the other.

Within these primary visual areas, two other characteristics are described. Firstly, spatial relationships between elements of the visual scene are retained by the anatomical organization of eye projections (retinotopy), which might have suggested that the primary visual cortex operated like a screen on which retinal signals were projected, sustaining the phenomenon of optic projection of the visual world onto the retina. Secondly, these projections do not lead to an isomorphism between the external space and the space represented in the visual cortex: the central areas of the visual field are largely over-represented on the cortical surface (central magnification). This central magnification reflects the retinal topography, which shows a highly heterogeneous quantitative and qualitative distribution of the photoreceptors: the increased density of cones in the center of the retina (fovea) provides a maximum visual acuity which drastically decreases in peripheral vision (see visual acuity curve according to different retinal eccentricities in relation to the fovea: Fig. 1A). Therefore, the image reconstitution projected onto the cortical surface is prone to an apparent deformation privileging the fovea to the detriment of peripheral areas (Fig. 1C).

In order to have a real precise vision in the entire visual field (as usually experienced by a healthy individual), one thus needs to orientate the fovea to different spatial points and incorporate these different snapshots into one. In fact, without being aware of it, a human has at least 5 spontaneous saccadic eye movements per second (Fig. 1B: spontaneous eye movements in the visual field during the simple observation of a person's face for 3 min [1]), with a treatment of the visual information processed mainly during the short time period between ocular saccades. Altogether, these three characteristics suggest that the cortical representation of the visual scene within the primary visual cortex is deformed in favor of the representation of what is currently seen by the fovea, shared between hemispheres and unstable because renewed at each saccadic eye movement.

2. Visual perception is based on a distributed neural network

This visual information arrives in the primary visual area, entry point to the cortical level, and is then distributed towards other

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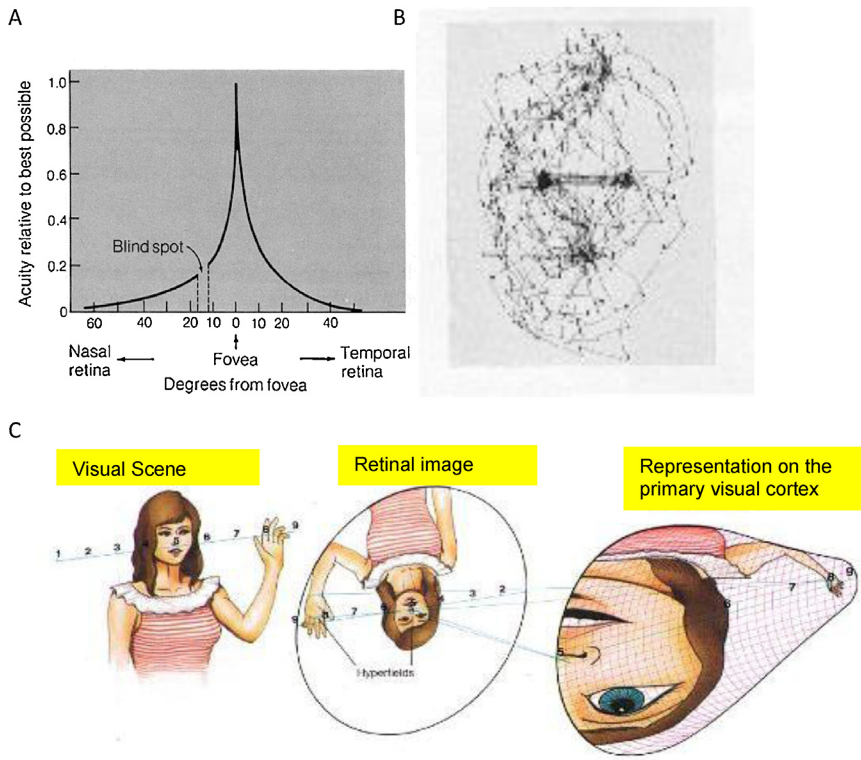

Fig. 1. Organization of the visual system. A. Visual acuity function for different retinal eccentricities. B. Spontaneous displacements of the eyes on the visual scene during a simple 3-minute observation. From [1]. C. Illustration of cortical central magnification.

visual areas for further processing. Today, we differentiate more than thirty visual areas, with more or less specialized contributions. In fact, some are more specialized in the processing of shapes, movements, colors or depth. The visual cortex can be described as a mosaic of strongly interconnected areas, each contributing to the processing of the visual scene. There is evidence of a global organization of these specialized areas according to two anatomical pathways. One occipito-temporal pathway, called the ventral stream, is essentially specialized in the analysis of the properties of visual objects in order to identify them (shapes, color, texture…). Another one, the occipito-parietal pathway, called the dorsal stream, is dedicated to the processing of the spatial properties of objects, i.e. their position, size and movements: all elements required to perform spatially-guided gestures. This fourth characteristic implies that one should consider the processing performed by the cortical visual system as a fragmentation of the visual world, decomposing not only the global scene but also each of the objects.

3. Which mechanisms bring a coherent visual perception?

These neurophysiological characteristics strongly contrast with the subjective experience of each person. In fact, our vision does not give us the impression to "jump" with each eye movement, or that the central part of the visual field is dilated, and finally we do not experience separately the different physical properties of the objects seen. The defined color of the apple I am visualizing is identical to the one I am grasping, it does not change size according to the position of my stare, and its perception is continuous when I move my eyes from the left to the right. What binds the different pieces of information coming from the same static or mobile objects, over time and through continuous eye movements? Several, non-exclusive, hypotheses were brought forward to explain how a unique or unified subjective visual experience does in fact emerge from this type of brain processing. Among them, the hypothesis attracting the most attention promotes the synchronization between the activities of the different neurons involved in the analysis of the different visual properties of a given object. It seems possible that visual elements received during the same visual fixation could benefit from some type of synchronization, even if they each have intrinsic processing delays (e.g. localization is treated faster than color [2] which, in turn is treated faster than shapes). Another hypothesis is the existence of high-level representational maps. In the posterior parietal cortex, association areas perform a spatiotemporal synthesis of the different snapshots. As a matter of fact, we find in those areas neurons that retain the memory trace of the position of important elements perceived in the visual scene by maintaining and updating their representation on oculocentric maps renewed at each new eye movement (visuospatial working memory).

4. The dorsal stream is the neural substrate of visuospatial working memory

Contrarily to retinotopic representations of the ventral stream that code and analyze with each new eye movement the information newly presented on the fovea and that overwrite the information previously processed during the former visual fixation, the oculocentric "priority maps" of the dorsal stream represent visual information:

- via an "activation level" attributing it a degree of importance (either because it is physically salient [for example, the onset of a new stimulus in the visual scene or strong luminance], or because it corresponds to an information needed for the ongoing task);

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